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BIRD ASSEMBLAGE STRUCTURE IN THE DESERT PUNA IN AREAS WITH DIFFERENT DISTURBANCE ACTIVITY OF A SUBTERRANEAN HERBIVOROUS RODENT

Estructura de la comunidad de aves en la Puna Desértica en áreas con diferentes niveles de actividad perturbadora de un roedor herbívoro subterráneo

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ABSTRACT: Herbivorous subterranean rodents, such as *Ctenomys mendocinus* (tuco-tuco), have a significant impact on vegetation cover and composition. This study aimed to examine the indirect influence of tuco-tucos on bird populations and assemblages in the southernmost region of the desert Puna. In a shrub-steppe community, at an altitude of between 3,000 and 3,100 m.a.s.l., bird surveys were conducted from February 2001 to October 2004. Transects of 50 m in length and 40 m in width were established: 56 located in highly disturbed patches and 53 in patches with low disturbance by tuco-tucos. Our results show that areas with higher disturbance by tuco-tucos are associated with a decrease in bird abundance (93 individuals in disturbed areas vs. 226 in undisturbed areas) and lower species richness (6 species in disturbed areas vs. 11 in undisturbed areas).

KEYWORDS: desert Puna, ecological engineers, *Ctenomys mendocinus*, Trophic cascade, bird assemblages.

RESUMEN: Los roedores subterráneos herbívoros como *Ctenomys mendocinus* (tuco-tuco), tienen un impacto significativo en la cobertura y composición de la vegetación. Este estudio tuvo como objetivo examinar la influencia indirecta de los tuco-tucos en las poblaciones y ensambles de aves del extremo sur de la Puna desértica. En una estepa arbustiva, a una altitud de entre 3.000 y 3.100 m.s.n.m., se realizaron muestreos de aves entre febrero de 2001 y octubre de 2004. Se establecieron transectos de 50 m de largo y 40 m de ancho: 56 ubicados en parches altamente perturbados y 53 en parches escasamente perturbados por los tuco-tucos. Nuestros resultados muestran que las áreas con mayor perturbación por tuco-tucos están asociadas con una disminución en la abundancia de aves (93 individuos en áreas perturbadas vs. 226 en áreas no perturbadas) y una menor riqueza de especies (6 especies en áreas perturbadas vs. 11 en áreas no perturbadas).

PALABRAS CLAVE: Puna desértica, ingenieros ecológicos, *Ctenomys mendocinus*, cascada trófica, ensambles de aves.

1. Introduction

Tuco- tucos (*Ctenomys* genus) are subterranean hystricognath rodents that occur throughout a wide range of environments in the South Cone of South America (Reig *et al*., 1990; Galiano & Kubiak, 2021). *Ctenomys* is one of the most speciose genera among mammals, and the most speciose among subterranean rodents, with 64 living species currently recognized (D'Elía *et al*., 2021). These rodents are strict herbivores that prefer to feed mainly on grasses (Madoery, 1993; Rosi *et al*., 2003; Lopes, 2021), but that also feed on forbs, shrubs and cacti when grasses are scarce (Rosi *et al*., 2003). Spatially, the individuals show an aggregate distribution, and their burrow systems have entrances, soil mounds and feeding holes (Pearson, 1951; Reig *et al*., 1990). The activity (feeding and burrowing) of these subterranean rodents affects plant cover, abundance of plants as well as soil nutrient concentration (Malizia, *et al*. 2000; Campos *et al*., 2001; Galiano *et al*., 2014). There is even a lizard of the genus *Liolaemus* (*L. eleodori*) that is known to be closely associated with *Ctenomys* burrows in the high Andes (Barrionuevo & Abdala, 2018).

One of the species of the genus *Ctenomys* occurring in Argentina is *C. mendocinus*. This species has a very strong effect on vegetation in a large part of its range (Tort *et al*., 2004; Lara *et al*., 2007; Albanese *et al*., 2010; Andino & Borghi, 2017; Bongiovanni *et al*., 2019; Borghi *et al*., 2020). At the southern end of the Puna desert, previous research showed that this species feed on almost all plant species in this environment (Rosi *et al*., 2003), and that their foraging activity reduces the cover of grasses, herbs and palatable shrubs, and indirectly favors dominance of the unpalatable shrub *Artemisia mendozana* (sagebrush) (Lara *et al*., 2007; Andino & Borghi, 2017). Moreover, in patches inhabited by this rodent, sagebrush plants have higher seed production and larger seed size (Andino & Borghi, 2017), probably because of relaxation of competition with other shrubs removed by *Ctenomys* foraging. Damage produced by their feeding behavior can cause the death of shrubs (Lara *et al*., 2007) and more commonly of grasses (C. Borghi, personal observation). Additionally, the presence of *C. mendocinus* has been observed to positively affect *Liolaemus ruibali*, increasing lizard abundance and enhancing their escape performance in the desert ecosystem (Bongiovanni et al., 2023).

We hypothesized that modifications of plant cover induced by herbivory from *C. mendocinus* generate effects on vegetation and indirectly on other taxa (e. g. invertebrates, birds, and mammals). Within this framework, we conducted a mensurative study to investigate the structure of the bird assemblage in a shrub-steppe community at the Desert Puna, examining areas with different disturbance activity of the subterranean rodent C. *mendocinus*. Our aims were to test the following predictions: 1) Bird abundance differs between patches heavily disturbed by *Ctenomys* and those relatively undisturbed, 2) bird species richness and diversity differ between heavily disturbed patches and those relatively undisturbed by *Ctenomys*, and 3) rank-abundance curves of bird species differ between patches that are heavily disturbed and those that are relatively undisturbed by *Ctenomys*.

2 Materials and methods

2.1 Study area

This study was conducted in Don Carmelo Multiple Use Private Reserve, a protected area of about 44,000 ha, located in La Invernada valley (31° 10'S, 69° 46' W), in San Juan province, Argentina (Figure 1). The study area is located in the southernmost extent of the Puna ecoregion, a desert environment at an elevation of > 3,100 m (Ellenberg, 1979; Matteucci, 2012). Vegetation is composed of low xerophytic shrubs and grasses (i.e., a shrub-steppe environment), with a large amount of bare soil (Márquez, 1999; Lara *et al*., 2007; Ripoll & Martínez Carretero, 2019). The climate of Puna at this latitude is dry, cold, with a wide daily temperature range, and primarily summer rainfall. The mean annual temperature is 8.15 °C, maximum absolute temperature is 26 °C, and minimum absolute temperature is -22 °C. Precipitation is about 100 mm/year, and snowfall occurs mainly between May and October with thickness up to 50 cm. Snow usually remains on the ground for no longer than 15 days (Andino & Borghi, 2017).

The most abundant herbivores occurring in the reserve are guanacos (*Lama guanicoe*) and the subterranean rodent *Ctenomys mendocinus*, locally called tuco-tuco. *C. mendocinus* are subterranean hystricognath rodents with a mass of 108-253 g, that dwell in areas ranging from 400 m to 3,200

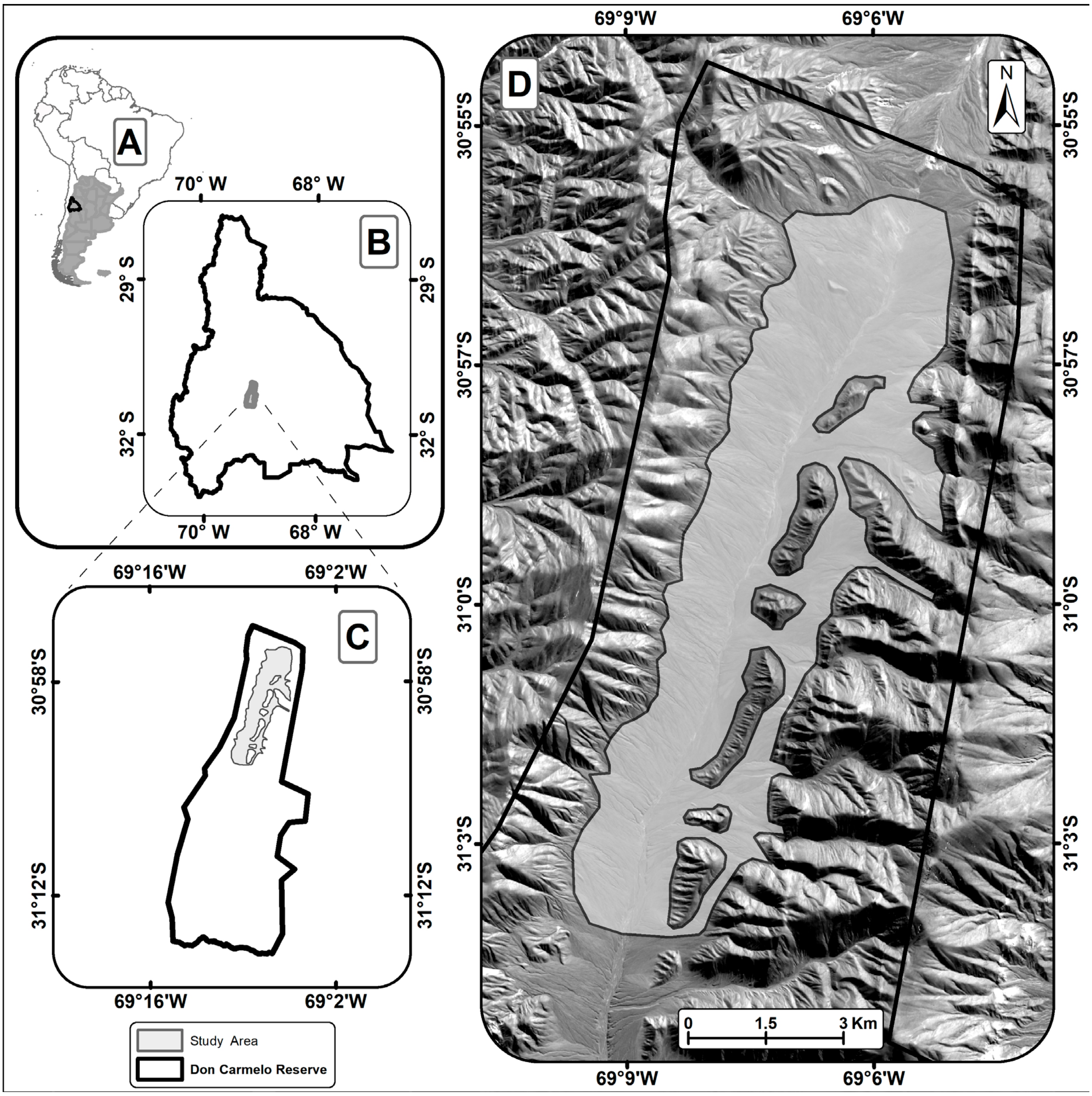

Figure 1. Location of the study area at the Don Carmelo Multiple Use Private Reserve in the south of Puna, San Juan Province, Argentina. Legend: a) Location of Argentina (in gray) within South America; b) Detail of the location of the Reserve (in gray) in the province of San Juan (Argentina); c) Reserve delimited by a continuous black line showing the study area in gray; d) Detail of Don Carmelo Multiple Use Private Reserve delimited by a continuous black line showing the study area in gray.
Figura 1. Ubicación del área de estudio en la Reserva Privada de Usos Múltiples Don Carmelo, en el sur de la Puna, provincia de San Juan, Argentina. Leyenda: a) Ubicación de Argentina (en gris) dentro de Sudamérica; b) Detalle de la ubicación de la Reserva (en gris) en la provincia de San Juan (Argentina); c) Reserva delimitada por una línea continua negra que muestra el área de estudio en gris; d) Detalle de la Reserva Privada de Usos Múltiples Don Carmelo delimitada por una línea continua negra que muestra el área de estudio en gris.

m.a.s.l. in arid and semi-arid environments of western Argentina (Rosi *et al*., 2005). *C. mendocinus* are strict herbivores, primarily consuming woody plants, but also feeding on grasses when available (Rosi *et al*., 2003), creating discrete patches through their intense herbivory, characterized by an increase in bare soil cover and a decrease in grass and shrub cover (Andino & Borghi, 2017, Borghi *et al*. 2020) (Figure 2). The area of these disturbed patches ranges from around 700 to 20,000 m^2. *C. mendocinus* home range depends on sex and locality, ranging from 12 to 43 m^2 (Rosi *et al*., 2005). In Don Carmelo Multiple Use Private Reserve, density of tuco-tucos ranges from 3.3 to 11.7 / ha (Borruel, 2013), with this burrowing activity also affecting soil nutrient concentration (Lara *et al*., 2007).

The study site was located on a high-altitude plateau, situated between the north-south oriented Sierra del Tigre and Sierra de la Invernada mountain ranges. Spanning approximately 4 km in width (west to east) and 15 km in length (north to south), this plateau maintains a consistent elevation ranging from 3,000 to 3,100 m.a.s.l. Such uniformity ensures comparable climatic and environmental conditions across all sampled transects, providing a stable context for our study. Within this expanse, patches are found in various states of disturbance ranging from very old patches, where vegetation is in the process of recovering, to patches where disturbance activity by tuco-tucos has been very recent. For this study, we selected only those patches that were either highly disturbed (but not in a recovery process) or relatively undisturbed (undisturbed) by *C. mendocinus*. In the disturbed patches, the abundance of burrow holes was approximately 9.6 times greater than in the undisturbed ones, soil mounds were about 7.4 times more prevalent, and plant cover was 55 % less than in undisturbed patches (Table 1).

Figure 2. Photos of *Ctenomys mendocinus* and its effect in the Don Carmelo Multiple Use Private Reserve landscape. a) Close-up of a *C. mendocinus* emerging from its burrow. b) Landscape with a *C. mendocinus*, illustrating the animal in its broader ecological context. c) Detail of *Lycium chanar* branches diagonally cut by the foraging activity of *C. mendocinus*. The distinct beveled cuts indicate the species' characteristic feeding method, underlining its influence on local flora. d) New *C. mendocinus* surface activity: a view of an area with two mounds of soil. e) Less disturbed habitat, offering a visual contrast to areas with higher levels of disturbance from *C. mendocinus* activity. f) Area heavily disturbed by *C. mendocinus* activity, showing the changes in the landscape resulting from their activity.

Figura 2. Fotos de Ctenomys mendocinus y su efecto en la Reserva Privada de Uso Múltiple Don Carmelo. a) Primer plano de un C. mendocinus emergiendo de su cueva. b) Paisaje con un C. mendocinus, mostrando al animal en su contexto ecológico. c) Detalle de ramas de Lycium chanar cortadas a bisel por C. mendocinus. Los cortes biselados son distintivos de la especie. d) Nueva actividad superficial de C. mendocinus: vista de un área con dos montículos de suelo. e) Hábitat menos afectado, ofreciendo un contraste visual con áreas de mayor perturbación por la actividad de C. mendocinus. f) Área fuertemente alterada por la actividad de C. mendocinus, mostrando los cambios en el paisaje resultantes de su actividad.

Table 1. Summary of Generalized Linear Models (GLM) assessing differences between patches disturbed by *Ctenomys* and undisturbed ones. The variables measured were burrow openings, soil mounds, and plant cover. Presented are the estimated means and 95 % confidence intervals (CI) for disturbed and undisturbed patches, statistical test values (z for count data, t for continuous data), Akaike Information Criterion (AIC), and the percentage of deviance explained by the models.
Tabla 1. Resumen de Modelos Lineales Generalizados (GLM) que evalúan diferencias entre parches perturbados y no perturbados por Ctenomys. Las variables medidas fueron número de bocas de galerías, número de montículos de suelo y cobertura vegetal. Se presentan las medias estimadas e intervalos de confianza del 95 % (IC), valores de pruebas estadísticas (z para datos de conteo, t para datos continuos), criterio de información de Akaike (AIC) y el porcentaje de la varianza explicada por los modelos.

Variable	Estimator	Disturbed	Undisturbed	Statistical Test	AIC	Explained Deviance
Burrow holes	Mean	34.60	3.60	z: -5.038	214.3	38.1 %
	Conf. Interv.	19.06-62.82	1.88-6.88	p: <0.0001		
Soil Mounds	Mean	18.27	2.47	z: -8.978	178.2	64.1 %
	Conf. Interv.	14.60-22.88	1.70-3.59	p: <0.0001		
Plant Cover	Mean	11.59	20.81	t: 6.834	167.5	62.5 %
	Conf. Interv.	9.64-13.50	18.86-22.80	p: <0.0001		

2.2 Field methods

Fieldwork was conducted from February 2001 to October 2004. In February 2001, sampling was carried out to characterize the plant cover, as well as to quantify the abundance of mounds and burrow holes created by *Ctenomys mendocinus*. This sampling was performed across two distinct types of areas: those heavily disturbed (disturbed) by the activities of *C. mendocinus* and those that remained relatively undisturbed (undisturbed). The degree of disturbance by *C. mendocinus* on the vegetation was assessed visually, ensuring consistency in our categorization of each patch. To accurately describe this influence, we randomly established thirty transects, each measuring 30 m in length, across both disturbed and undisturbed sites. Specifically, fifteen transects were placed in areas heavily disturbed by tuco-tucos, and fifteen were situated in relatively undisturbed patches (Figure 2). For each transect, we collected samples from ten plots, each covering an area of 2 m² and spaced 1 m apart, resulting in a total sampled area of 20 m² per transect. The sampling unit was the transect.

To assess the influence of *Ctenomys mendocinus* on bird populations, fieldwork was conducted from February 2003 through October 2004. We selected two types of patches: (1) patches highly disturbed by tuco-tucos (with high density of holes [1.73 ± 0.11 /m^2, mean ± SE] and mounds [0.91 ± 0.03 / m^2];= “disturbed patches”), and (2) patches relatively undisturbed by *Ctenomys* (with low density of holes [0.18 ± 0.05 /m^2] and mounds [0.12 / ± 0.02 / m^2]; = “undisturbed patches”) Lara *et al.* (2007). We randomly selected 109 patches (with a diameter of 50 meters or larger) for this purpose, divided between disturbed (56) and undisturbed (53), ensuring each patch was represented by a single transect. These transects, 50 m in length and 40 m in width, were placed at least 200 m apart to minimize overlap in bird territories. Surveys were carried out during times of peak bird activity – in the early morning (7:30 am to 10:30 am) and late afternoon (4:30 pm to 7:30 pm) – across three seasons: summer (February 2003), autumn (May 2003), and spring (October 2004). Each transect was walked at a steady pace for 30 minutes by the same observer, who recorded sightings of bird species, identified with the help of the field guide by Narosky and Yzurieta (2003). The scientific and common names of the birds observed are listed in Table 2.

2.3 Data analysis

To describe and assess the ecological effect of *Ctenomys* activity on plant cover, burrow openings, and soil mounds, we employed Generalized Linear Models (GLMs) with appropriate error distributions for each type of data. Gaussian error distribution was used for the continuous variable of plant cover, whereas a negative binomial distribution was employed for the count data of burrow holes and soil mounds to accommodate overdispersion. We incorporated disturbance level as a fixed effect in all models to directly evaluate its ecological effect. The statistical analyses were performed in R (R

Table 2. Bird species observed in the desert Puna at Don Carmelo Multiple Use Private Reserve. Scientific and English common names, habitat used and main diet categories. Sources: (1) Fjeldså J & Krabbe 1990; (2) Ferrer *et al*. 2014; (3) Blendinger 2005; (4) Herzog *et al*. 2003; (5) Ipanaqué Panta 2014; (6) Cáceres-Polgrossi 2016; (7) Kelt *et al*. 2012; (8) Kelt *et al*. 2016; (9) Soto-Huaira *et al*. 2019; (10) Aramburu *et al*. 2007.
Tabla 2. Especies de aves observadas en la Puna desértica en la Reserva Privada de Usos Múltiples Don Carmelo. Nombres científicos y comunes en inglés, hábitat utilizado y principales categorías de dieta. Fuentes: (1) Fjeldså J & Krabbe 1990; (2) Ferrer et al. 2014; (3) Blendinger 2005; (4) Herzog et al. 2003; (5) Ipanaqué Panta 2014; (6) Cáceres-Polgrossi 2016; (7) Kelt et al. 2012; (8) Kelt et al. 2016; (9) Soto-Huaira et al. 2019; (10) Aramburu et al. 2007.

Order	Family	Species	Patch used	Common name	Habitat	Diet
Passeriformes	Tyrannidae	*Muscisaxicola cinereus*	Both	Cinereous ground-tyrant	High-Andean steppes, pre-Puna and nearby mountain stream	Insectivorous (1, 2)
Passeriformes	Tyrannidae	*Muscisaxicola maculirostris*	Both	Spot-billed Ground-tyrant	High- Andean and high elevation steppes, pre-Puna and Andean valleys	Insectivorous (3)
Passeriformes	Mimidae	*Mimus patagonicus*	Undisturbed	Patagonian mockingbird	Andean and Patagonian, arid and shrub steppes	Insectivorous (3)
Passeriformes	Emberizidae	*Geospizopsis plebejus*	Undisturbed	Ash-breasted Sierra-finch	High Andean steppes and high-altitude grasslands	Frugivorous-Insectivorous (4,5)
Passeriformes	Thraupidae	*Sicalis auriventris*	Undisturbed	Greater yellow finch	Puna and shrub steppes	Granivorous (6)
Passeriformes	Furnariidae	*Geositta cunicularia*	Both	Common miner	Open areas in Andes, Patagonia and pampas	Insectivorous (7,8)
Passeriformes	Furnariidae	*Geositta rufipennis*	Undisturbed	Rufous – banded miner	High-Andean steppes and high elevations	Insectivorous (7,8)
Passeriformes	Furnariidae	*Geositta isabellina*	Both	Creamy-rumped miner	High-Andean steppes and high elevations	Insectivorous (9)
Passeriformes	Furnariidae	*Asthenes dorbignyi*	Undisturbed	Creamy-breasted	Puna and shrub steppes	Insectivorous (8)
Charadriiformes	Charadriidae	*Oreopholus ruficollis*	Both	Tawny-throated dotterel	High Andean and Patagonian steppes	Insectivorous (8)
Charadriiformes	Thinocoridae	*Thinocorus rumicivorus*	Both	Least seedsnipe	Steppes, meadows and lakes in NW and Patagonia	Granivorous-Folivorous (10)

Core Team, 2021), utilizing the functions 'glm' for Gaussian models and 'glm.nb' for negative binomial models, provided by the *'stats'* and *'MASS'* packages (Venables & Ripley, 2002), respectively. Overdispersion was evaluated using the 'dispersiontest' function from the *'AER'* package (Kleiber & Zeileis, 2008). Additionally, we employed the *'emmeans'* package to estimate and interpret the fixed effects with their confidence intervals, thereby quantifying the magnitude of disturbance's influence.

We applied Generalized Linear Mixed Models (GLMMs; Zuur *et al*., 2009) with Poisson error distribution and Negative Binomial error distribution if variables exhibited overdispersion ($\hat{C} > 1$; Crawley, 2007) to analyze if *C. mendocinus* disturbance affects the abundance of all bird species occurring in the area. The response variable was abundance of all bird species, the explanatory variable was disturbance by *Ctenomys* (two levels: disturbed and undisturbed patches), and the random effect used was the month of survey (three levels: February, May and October). GLMMs were fitted using the glmer function from the *lme4* package (Bates *et al*., 2015). The significance of fixed and random effects was assessed using the likelihood ratio test (LRT; Bolker *et al*., 2008).

To determine the impact of *Ctenomys* disturbances on avian populations, we concentrated on species with total abundances greater than 20 individuals, analyzing data from months with significant recorded abundances. This approach aimed to enhance the statistical robustness of our intra-specific abundance comparisons, focusing on the effects of disturbances on four bird species: *Oreopholus ruficollis* and *Thinocorus rumicivorus* in February, and *Muscisaxicola cinereus* along with *Geositta cunicularia* in May. We encountered significant numbers of zero counts in our bird species abundance data, exceeding what standard Poisson or Negative Binomial distributions would predict, indicative of excess zeros. The data also exhibited over-dispersion, where variance surpassed the mean, suggesting that these standard models were insufficient for our analysis (Zuur *et al.*, 2012). To accurately assess the effect of *Ctenomys* disturbances, we employed Zero-Inflated models, which are adept at managing datasets characterized by excess zeros and over-dispersion. These models include two components: a logistic regression model that predicts the likelihood of zero counts, and a count model (Poisson or Negative Binomial) for the positive counts. Depending on the dispersion index ($\hat{C} > 1$; Crawley, 2007), we applied Zero-Inflated Poisson Models (ZIP) and Zero-Inflated Negative Binomial Models (ZINB) using the *pscl* package (Jackman, 2020) and the *lmtest* package (Zeileis & Hothorn, 2002). The significance of the disturbance effect as a fixed effect in our models was evaluated using the likelihood ratio test (LRT; Bolker *et al.*, 2008), enabling us to discern the effect of *Ctenomys* disturbances on bird species abundance.

To evaluate the differences in bird species richness and diversity in areas with varying levels of *C. mendocinus* activity, as well as to analyze the variations in the rank-abundance curves among these areas, we adopted a comprehensive analytical approach. We analyzed the entire dataset, incorporating all species recorded throughout the study period without omitting any due to low abundance. This comprehensive dataset underpinned the calculation of diversity indices, such as species richness, Shannon diversity, and Simpson diversity. Our approach ensured that the resultant diversity indices accurately reflect the full ecological complexity of both disturbed and undisturbed sites, without bias from species omission. As every patch type (disturbed by *Ctenomys* and undisturbed) had a different number of transects (56 and 53 respectively), we performed coverage-based rarefaction curves to estimate sampling completeness at each patch type (Chao *et al.*, 2014). Sample completeness refers to the proportion of total abundance or number of individuals in an assemblage that belong to the species represented in the sample (Chao & Jost, 2012).

In order to quantify the species diversity in disturbed and undisturbed sites, ${}^{0}D$, ${}^{1}D$ and ${}^{2}D$ metrics was used, which are parameterized by the Hill numbers 0, 1 and 2, respectively (Hill, 1973; Jost, 2006). The values of q are referred to as the “order” of the diversity measure. ${}^{0}D\alpha$ represents species richness ($q = 0$); ${}^{1}D\alpha$, Shannon diversity index, represents the number of common species ($q = 1$); and ${}^{2}D\alpha$, Simpson diversity index, represents the number of dominant species in a community ($q = 2$) (Jost, 2006). We used the function mcpHill (R package “*simboot*”) to compare diversities of patches highly disturbed by *Ctenomys* and undisturbed (Pallmann *et al.*, 2012; Scherer & Pallmann, 2017; Canty & Ripley 2019). We assessed statistical differences in species diversity by applying multiple contrast tests based on the resampling technique (Westfall & Young, 1993).

We characterized species diversity at both types of patches, building two types of integrated rarefaction and extrapolation curves (sample-size and coverage-based), with 95 % confidence intervals, obtained by a bootstrap method based on 1,000 replications using *iNEXT* package (Hsieh *et al.*, 2016). For sample-size curves, the maximum reference sample size (226 individuals) was used as a base sample size, and for coverage-based curves we standardized the samples to the maximum coverage for reference samples (100 %). Pielou’s evenness index (J) was calculated as a measure of equitability, i.e. the proportion of the diversity observed in each patch was assessed in relation to the maximum expected diversity (Magurran, 2004). These analyses were supplemented with bird species rank abundance curves for both types of patches using the Biodiversity R package (Kindt & Kindt, 2019).

Results are presented as mean ± standard error (SE) and, for null hypothesis testing, statistical tests were considered significant at $\alpha < 0.05$. All analyses were performed with R Software 3.6.1 (R Core Team 2019). Results are expressed as the untransformed mean ± SE.

3. Results

3.1 Differences in bird abundance between areas with high and low activity of C. mendocinus

We recorded a total of 319 birds at patches disturbed and undisturbed by *Ctenomys*. They belong to two orders, seven families, eight genera and 11 species (Table 2).

Birds (all species) were significantly less abundant (93 individuals, mean number of birds per transect: 1.66 ± 0.93) at disturbed patches with high levels of activity by *Ctenomys* compared to undisturbed patches (226 individuals, 4.26 ± 0.88 birds/transect) (GLMM, LRTtest $\chi 2 = 9.41$; df = 1; p = 0.0021). We found that total abundance was also influenced by the random factor (month; $p < 0.0001$). The most abundant recorded bird species included the insectivores *Muscisaxicola cinereus*, *Geositta cunicularia*, *Oreophollus ruficallis* and the granivore *Thinocorus rumicivorus*. Since these species exhibited a migratory abundance pattern, we compared their abundances between disturbed and undisturbed sites during periods when their numbers were sufficient for statistical comparison. The most frequently recorded bird species was *M. cinereus*, with observations of 62 individuals in undisturbed patches versus 50 in disturbed patches during May. Following this species were *G. cunicularia* in May, and *T. rumicivorus* and *O. ruficallis* in February, with each species' populations exceeding 19 individuals in a given month. The abundance of *M. cinereus* and *T. rumicivorus* was significantly different between undisturbed and disturbed patches by *Ctenomys*, but not that of *O. ruficallis* or *G. cunicularia* (Table 3). *M. cinereus* was more abundant at undisturbed than disturbed patches (mean 6.20 individuals/transect vs 3.85 respectively), and *T. rumicivorus* followed the same pattern (0.47 vs 0.06 respectively). *Ctenomys* did not affect the probability of absence of these four species (Zero-inflated models; Table 3). *Mimus patagonicus*, *Geospizopsis plebejus*, *Geositta rufipennis*, *Asthenes dorbignyi* and *Sicalis auriventris* were considered rare species because they were observed only in undisturbed patches and with low abundance (abundance < 4 individuals in all transects). For some cases, for instance for *G. rufipennis*, we observed only one individual over all study periods; and in the case of *S. auriventris*, we recorded three individuals just once on one transect.

3.2 Differences in bird species richness and diversity between areas with high and low activity of C. mendocinus

At undisturbed patches, we recorded 226 individuals among 11 species, and at disturbed patches we recorded 93 individuals among 6 species. Sampling completeness reached 99 % for undisturbed patches and 100 % for disturbed ones.

Table 3. Zero-Inflated Poisson Models (ZIP) and Zero-Inflated Negative Binomial Models (ZINB) were used to assess the effect of *Ctenomys* disturbance on bird abundance in the desert Puna of the Don Carmelo Reserve. Estimated coefficients, standard errors, z values, and p-values are provided for each model component. McFadden's R^2 is also presented, indicating the model's explained variability compared to the null model.
Tabla 3. Se utilizaron Modelos Poisson Inflados en Cero (ZIP) y Modelos Binomiales Negativos Inflados en Cero (ZINB) para evaluar el efecto de la perturbación por Ctenomys sobre la abundancia de aves en la Puna desértica de la Reserva Don Carmelo. Se proveen los coeficientes estimados, errores estándar, valores z y p para cada componente. También el R^2 de McFadden, indicando la variabilidad explicada por el modelo en comparación con el modelo nulo.

Bird species	Model / McFadden R^2	Component	Variable	Estimate	Std. Error	z value	p value	
T. rumicivorus February	ZIP 0.09	Count	Intercept	-28.607	0.7252	-3.945	<0.0001	***
			SituationUndisturbed	36.233	0.7798	4.646	<0.0001	***
		Zero-Inflation	Intercept	-6.472	104.399	-0.062	0.9510	
			SituationUndisturbed	7.737	104.400	0.074	0.9410	
O. ruficollis February	ZINB 0.04	Count	Intercept	25.237	0.3788	6.663	2.68e-11	***
			SituationUndisturbed	-0.4173	0.4370	-0.955	0.3400	
			Log(theta)	15.837	0.8865	1.787	0.0740	
		Zero-Inflation	Intercept	28.012	0.7283	3.846	0.0001	***
			SituationUndisturbed	-13.899	0.8418	-1.651	0.0987	
G. cunicularia May	ZINB 0.05	Count	Intercept	0.0822	36.889	0.022	0.9820	
			SituationUndisturbed	14.408	21.092	0.683	0.4950	
			Log(theta)	-18.952	42.055	-0.451	0.6520	
		Zero-Inflation	Intercept	0.9276	47.828	0.194	0.8460	
			SituationUndisturbed	-19.810	73.382	-0.270	0.7870	
M. cinereus May	ZIP 0.35	Count	Intercept	39.120	0.1414	27.662	< 2e-16	***
			SituationUndisturbed	-0.8835	0.1901	-4.648	3.35e-06	***
		Zero-Inflation	Intercept	2.485	1.041	2.387	0.0170	*
			SituationUndisturbed	-1.638	1.249	-1.311	0.1900	

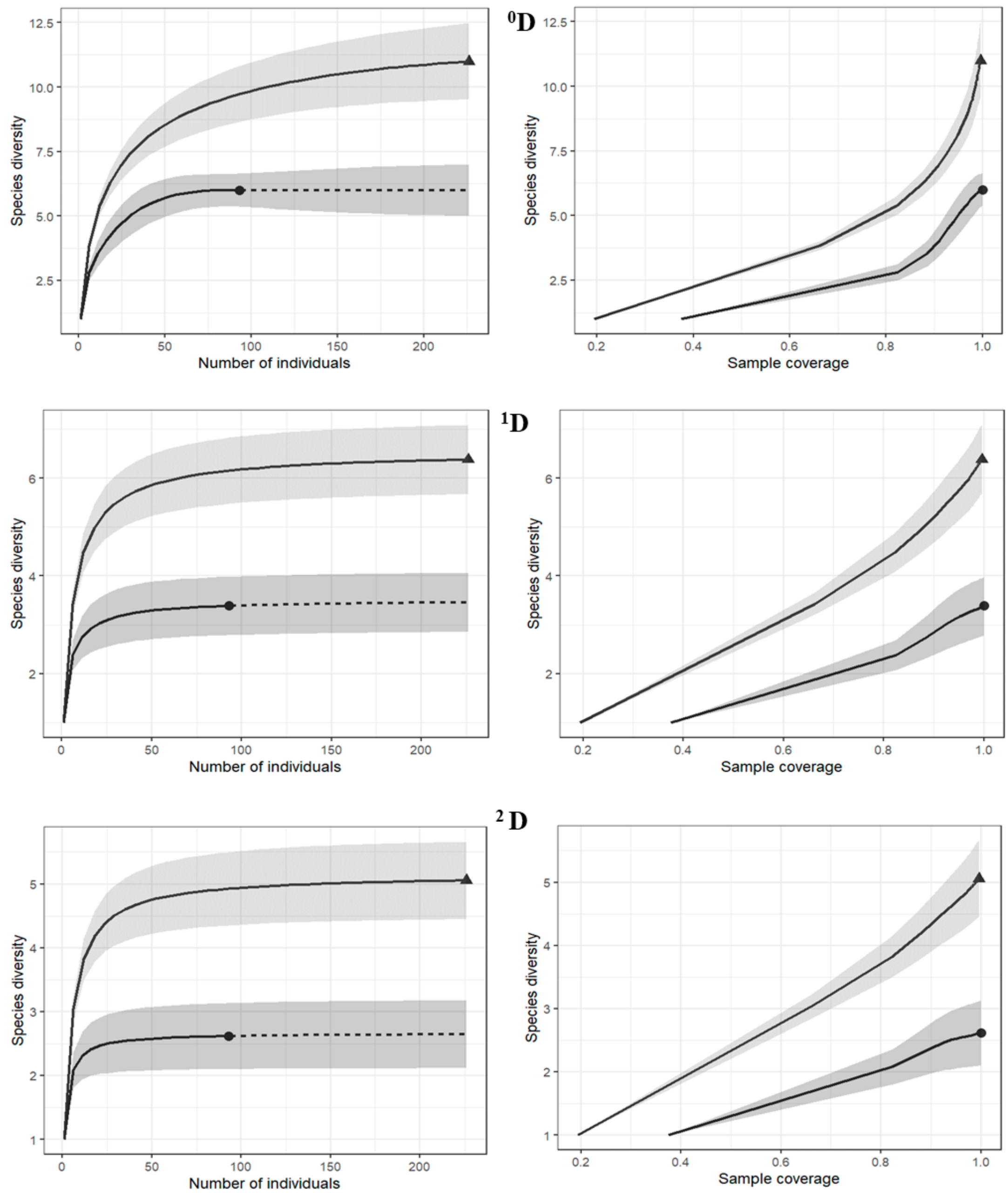

Figure 3. Comparison of sample-size-based (left panels) and sample-coverage-based (right panels) rarefaction and extrapolation for Hill numbers: q=0 (upper panels), q=1 (middle panels), and q=2 (lower panels) for patches with herbivory by Ctenomys (circle) and without herbivory (triangle). Observed samples are denoted by solid dots; rarefied segments are denoted by solid lines and extrapolated segments by broken lines. The extrapolation extends up to a maximum sample size of 226 individuals. The sample-coverage-based extrapolation extends to the coverage value of the corresponding maximum sample size. The 95 percent confidence intervals (shaded areas) were obtained by a bootstrap method based on 1000 replications.

Figura 3. Comparación de la rarefacción y extrapolación basadas en el tamaño de la muestra (paneles de la izquierda) y en la cobertura de la muestra (paneles de la derecha) para los números de Hill: q=0 (paneles superiores), q=1 (paneles medios) y q=2 (paneles inferiores) para parches con herbivoría por Ctenomys (círculo) y sin herbivoría (triángulo). Las muestras observadas están denotadas por puntos sólidos; los segmentos rarefactados están denotados por líneas sólidas y los segmentos extrapolados por líneas discontinuas. La extrapolación se extiende hasta un tamaño máximo de muestra de 226 individuos. La extrapolación basada en la cobertura de la muestra se extiende hasta el valor de cobertura del tamaño máximo de muestra correspondiente. Los intervalos de confianza del 95 por ciento (áreas sombreadas) se obtuvieron mediante un método de bootstrap basado en 1000 replicaciones.

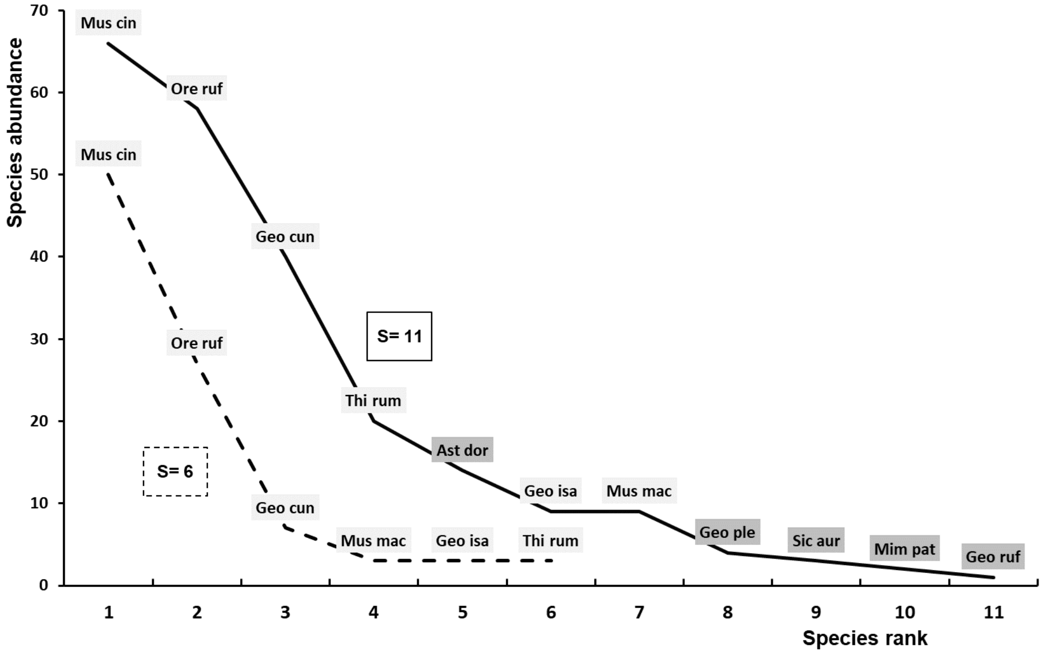

Figure 4. Rank-abundance curve for bird species recorded at patches with herbivory by *Ctenomys mendocinus* (dashed line), and without herbivory (solid line), at the Don Carmelo Multiple Use Private Reserve. For visualization purposes, species names are abbreviated by the first three letters of the genus and first three letters of the species epithet. Names highlighted in gray correspond to species present only at patches without herbivory.
Figura 4. Curva de rango-abundancia para especies de aves registradas en parches con herbivoría por Ctenomys mendocinus (línea punteada), y sin herbivoría (línea continua), en la Reserva Privada de Uso Múltiple Don Carmelo. Para fines de visualización, los nombres de las especies se abrevian con las primeras tres letras del género y las primeras tres letras del epíteto de la especie. Los nombres resaltados en gris corresponden a especies presentes solo en parches sin herbivoría.

Table 4. Diversity parameters estimated through Hill numbers (^qD) for patches disturbed and undisturbed by *Ctenomys mendocinus* in the Puna desert.
Tabla 4. *Parámetros de diversidad estimados mediante números de Hill (^qD), para parches perturbados y no perturbados por Ctenomys mendocinus en el desierto de la Puna.*

Patches	Observed	Estimated		Confidence interval	
		asymptote	S.E	95 % lower	95 % upper
Disturbed					
Species richness (^0D)	6	6	0.37	6.00	6.90
Shannon diversity (^1D)	3.38	3.48	0.33	3.38	4.14
Simpson diversity (^2D)	2.61	2.66	0.26	2.61	3.17
Undisturbed					
Species richness (^0D)	11	11.49	1.31	11.02	19.41
Shannon diversity (^1D)	6.38	6.53	0.38	6.38	7.29
Simpson diversity (^2D)	5.05	5.14	0.35	5.05	5.83

Using Hill numbers (i.e., the effective number of species), our evidence confirmed that undisturbed patches were significantly more diverse than those disturbed by *Ctemomys* (^{0}D, p = 0.01; ^{1}D, p = 0.04; ^{2}D, p = 0.05) (Table 4 and Figure 3). At patches undisturbed we found one species represented by one individual (singleton species) and one species represented by two individuals (doubleton species). However, at disturbed patches we did not find any singletons or doubletons. The sample-size rarefaction and extrapolation curves (base sample size= 226) showed a consistent pattern in all indexes, with the diversity curve for undisturbed patches above the curve of disturbed patches for all three parameters (Figure 3).

By standardizing both patches to the same sampling effort (sample coverage 1.00), we found that, at both types of patches, the coverage-based curves give the same ordering of diversity (^{0}D > ^{1}D > ^{2}D) with higher diversity at patches without disturbance than at disturbed patches (Figure 3). Pielou's evenness shows that patches free from disturbance by *Ctenomys* were more similarly distributed than disturbed patches (J' = 0.77 and J' = 0.68, respectively).

3.3 Differences in the rank-abundance curves of bird species between areas with high and low activity of C. mendocinus

The rank-abundance curve showed that *Muscisaxicola cinereus* was the most abundant bird species at both types of patches. At undisturbed patches, *Geossita rufipennis* had the lowest abundance, while *Thinocorus rumicivorus* had the lowest abundance at disturbed ones (Figure 4). The declining species-rank curve indicates that there is great dominance of the most abundant species at both types of patches. *A. dorbingnyi* was recorded only at undisturbed patches, as well as the least abundant species *S. auriventris*, *M. patagonicus* and *G. rufipennis* (Figure 4).

4. Discussion

Plant species abundance differs between areas relatively undisturbed and highly disturbed by *Ctenomys mendocinus* (Tort *et al*., 2004; Lara *et al*., 2007; this study). The burrowing activity of *Ctenomys* indirectly influences plant reproductive output (Andino & Borghi, 2017), emergence, and reproductive strategy (Borghi *et al*., 2020), demonstrating the complex interactions within these ecosystems.

Complementing this, Bongiovanni *et al.* (2023) have reported that disturbances caused by *C. mendocinus* positively influence the abundance of *Liolaemus ruibali*, likely due to an increase in shelter and potential enhancement in food resource availability. The observed decrease in flight initiation distance of *L. ruibali* in disturbed areas suggests that the habitat modifications by *C. mendocinus* reduce the perceived predation threat, allowing these lizards to tolerate closer presence of predators.

Extending these findings to avian communities reveals contrasting effects. Bird abundance and species richness were found to be lower in disturbed patches compared to undisturbed ones, emphasizing the variable impact of *C. mendocinus* disturbances across taxa. In the high-altitude shrub-steppe of the Puna desert, the abundance of *Muscisaxicola cinereus* and *Thinocorus rumicivorus* was notably reduced in areas disturbed by *Ctenomys*. Though not statistically significant for other bird species, a general trend of lower abundance in disturbed patches was observed, suggesting a nuanced impact of these disturbances on various species.

Ctenomys disturbance affected several parameters of the bird assemblage, leading to higher Hill numbers at patches with lower levels of activity. This aligns with findings from Utsumi *et al.* (2009), indicating that herbivory influences community dynamics. However, unlike Utsumi *et al.* (2009), who focused on predator community composition, our findings highlight effects on species richness, diversity, and overall bird abundance in disturbed patches, suggesting a bottom-up trophic cascade induced by *C. mendocinus* activity.

Hill numbers showed that patches highly disturbed by *Ctenomys* led to a loss of species richness of up to 31 %, whereas total loss of abundance was 59 %. This means that patches with this rodent allow for only a limited number of bird species with low abundances. This could be the consequence of the effects of herbivory and other *Ctenomys* disturbances on several levels of the community. *Ctenomys* activity affects several aspects of the ecosystem. The composition and structure of vegetation are negatively affected by *Ctenomys*, mainly by their foraging, but also by their burrowing activity. *Ctenomys* damage produced by their feeding behavior can cause the death of shrubs (Lara *et al*., 2007) and more frequently of grasses (Borghi personal observation). Borruel (2013) also detected, in *Ctenomys* disturbed patches, a decrease in the number of arthropod families, and in the number of individuals in almost all arthropod assemblages studied in the study area. These changes probably affect the availability of food for at least insectivorous birds, thus affecting the entire community (i.e., a community-level cascade; Polis, 1999; Marquis, 2010). Rank-abundance curves for bird species show similar results, with *Ctenomys* disturbance reducing abundance and richness of bird species. This impact results in a less ecologically complex bird assemblage in patches with *Ctenomys* disturbances.

A hypothesis that could elucidate the observed disparities in bird populations within areas disturbed and undisturbed by *C. mendocinus* posits that *Ctenomys* disturbance directly diminish plant abundance. This reduction likely leads to a scarcity of crucial resources for birds, such as seeds, plant leaves, and the insects that rely on this vegetation. Consequently, the depletion of these food sources may precipitate a decline in bird abundance and diversity. Another hypothesis that could explain the decrease in the abundance and richness of birds in the area disturbed by *Ctenomys* could consider that the decrease in vegetation cover by *Ctenomys* activity might impact the birds' perception of predation risk. In contrast to reptiles like *L. ruibali*, which potentially benefit from the proliferation of burrow holes as shelters from predators, birds may perceive the reduced vegetation cover as an increase in their vulnerability to predators, due to a perceived scarcity of safe refuges. This heightened exposure may enhance their perceived predation risk, leading to a reduction in both the number and variety of birds in these areas. Confirming any of these hypotheses would contribute to the limited body of research on inverse trophic cascades caused by herbivorous mammals (Roinine *et al*., 1997; Pringle *et al*., 2007; Tabuchi *et al*., 2011).

In summary, our study represents a novel finding, indicating the potential occurrence of a bottom-up trophic cascade initiated by a small rodent, which exerts influences on higher trophic levels including birds, resulting in changes at both, the species and community levels. It is noteworthy that these influences may be further amplified by the low primary productivity observed in the studied environment, as previously suggested by Pringle *et al*. (2007).

Our findings emphasize the importance of conducting further experimental studies to gather evidence supporting the proposed mechanisms underlying this potential trophic cascade, particularly regarding how the activity of *Ctenomys* could influence bird abundance, diversity, and other community parameters. The potential cascading effects and other interactions they may induce could have comparable impacts to those observed in other systems following the loss of top predators or large herbivorous mammals (Estes *et al*., 2011), highlighting the critical need for their study and conservation. Moreover, considering the ongoing decline of many *Ctenomys* species (with 42 % classified as threatened; SAyDS–SAREM, 2019), we emphasize their ecological value due to the effects of these subterranean herbivorous rodents on their respective communities. Further research is necessary to unravel the mechanisms driving the influence of *Ctenomys* on bird abundance and diversity. This can be achieved through a combination of observational and manipulative experimental studies, which will provide insight into the causal role of this subterranean rodent in the ecosystem. For instance, investigating the differences in resource availability (plants and prey) and their relationship with cascading effects on birds, as well as implementing simulated herbivory treatments to manage plant abundance and study resulting modifications in the bird assemblage, among other relevant factors. Overall, it is essential to continue conducting research to gain a comprehensive understanding of the ecological dynamics associated with *Ctenomys* and their potential role in generating cascading effects. This research will help us shed light on their functional role within the ecosystem.

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Data Availability

The dataset associated with this article is available in the "Repositorio de Datos de Investigación CONICET Digital" at the following link: http://hdl.handle.net/11336/237990

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Authorship Contribution Statement

Carlos E. Borghi conceived and designed the study. Natalia Andino, Viviana Fernández, and Stella M. Giannoni analyzed the data. C. E. Borghi, N. Andino, V. Fernández, and S.M. Giannoni interpreted the data. C.E. Borghi and S.M. Giannoni drafted the manuscript. C.E. Borghi reviewed and edited the manuscript. All authors gave final approval of the version to be published.